CONSERVATION BIOLOGY OF THE GYRFALCON (*FALCO RUSTICOLUS*) IN NORTHERN FENNOSCANDIA

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Abstract.—Northern Fennoscandia is one of the few areas in the world where there are systematic and comparable data on the population density and breeding of the Gyrfalcon during the last 150 years. I have studied population ecology and conservation biology of the species in Finland and nearby areas on the Swedish and Norwegian side of the border since the early 1990s by searching for and monitoring all territories in a defined area. The study area is relatively flat with gently sloping fell-mountains covered by pine and birch forests, the highest tops reaching ca. 1,000 m above the sea level.

Ptarmigan form almost 90% of the prey items during the breeding season, about three quarters of them being Willow Ptarmigan (*Lagopus lagopus*) and one quarter Rock Ptarmigan (*L. muta*). These two species offer almost the only available food for falcons during winter. The density of Willow Ptarmigan, the main prey species, has varied nine-fold during late winter and early spring from 2000 to 2010, and this fluctuation has had a marked effect on both the percentage of pairs starting to breed and on breeding success of the total population.

Territory occupation varied markedly. Of the 25 territories surveyed every year from 2000 to 2010, 12 had breeding pairs every second year or more often, but one-quarter of them were occupied only once or twice during that study period. The median frequency of territory occupancy by a breeding pair was four in 11 years. The percentage of territories occupied by breeding pairs increased from 30–40% to 50–55% from 2002 to 2007 (when Willow Ptarmigan density increased threefold) and reached its maximum two years after the prey population high. In 2009–2010, when the density of Willow Ptarmigan population was exceptionally low, a nine fold decrease from the peak five years earlier, only one-tenth of the Gyrfalcon territories were occupied by breeding pairs. In mid-winter, 90% of the territories were occupied by falcons during the ptarmigan population high, but only one-half of them during the population low.

Among 619 records of territory occupancy during the breeding season, all study years combined, pairs began nesting 214 times (34.6%). Of the nesting attempts, 36 (17%) appeared to fail during the egg-stage, but only four (2%) after hatching. Thus, 81% of the pairs that laid eggs were successful in raising at least one young. The number of young per brood varied from one to five, with 2.93 young per successful nesting, on average, and 1.34 young per occupied territory (the respective figures for the main study period 2000–2010, with almost all territories surveyed annually, were 2.98 and 1.40). The mean annual number of big young (probably fledged) per successful pair varied from 2.0 to 3.3 during the main study period, and that per occupied territory from 0.2 to 2.2., reflecting the population fluctuations of Willow Ptarmigan density.

Breeding and non-breeding territorial adults tended to be faithful to their territories from year to year. Individual identification based on plumage characteristics and behavior suggested that adult females bred or occupied their territories for as long as eight years.

The density of Gyrfalcon territories in my study area varied annually from ca. 1.7 to 2.7 per 1,000 km^2 since the late 1990s. The total number of breeding pairs in Fennoscandia, including Norway, Sweden, Finland and the Kola Peninsula, Russia, has been estimated at ca. 600–1,200 pairs, twice as many as thought less than a decade ago, due to a marked increase in the Norwegian estimate. The current density of the Gyrfalcon population is probably at the same general level as 150 years ago. Earlier estimates of a long-term 80% decline are exaggerations due to methodological flaws, brief study periods, and surveys restricted to the classical sites. Those estimates did not take into account the facts that Gyrfalcon pairs do not breed every year and have alternative nests.

An apparent population decline of ptarmigan and unintentional disturbance of breeding birds are the most critical threats to the Fennoscandian Gyrfalcon population. *Received 4 August 2011, accepted 26 October 2011.*

Koskimies, P. 2011. Conservation biology of the Gyrfalcon (*Falco rusticolus*) in northern Fennoscandia. Pages 95–124 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov (Eds.). Gyrfalcons and Ptarmigan in a Changing World, Volume II. The Peregrine Fund, Boise, Idaho, USA. http://dx.doi.org/10.4080/gpcw.2011.0213

Key words: Gyrfalcon, Fennoscandia, Finland, territory occupation rate, breeding success, dependence on ptarmigan, long-term population changes.

The Gyrfalcon has a long and exceptional history in connection with mankind in northern Europe. It has been the most valued species among European falconers at least since the beginning of the second Millennium. In his famous book, *De Arte Venandi cum Avibus,* Frederick II of Hohenstaufen (ca. 1248) praised the Gyrfalcon as follows (translated by Wood and Fyfe 1943): "Out of respect for their size, strength, audacity, and swiftness, the gerfalcons shall be given first place in our treatise…", and "…in our experience the rare white varieties from remote regions are the best." According to Frederick II, Gyrfalcons were brought to Central Europe from "…a certain island lying between Norway and Gallandia, called in Teutonic speech Yslandia." He meant Iceland. Three centuries later, lack of proper knowledge, combined with imagination about the supernatural powers of the Gyrfalcon, led the first great historian of the Nordic folks, Olaus Magnus (1555), to exaggerate that the Gyrfalcon is strong and furious enough to rush to hunt up to five Common Cranes (*Grus grus*) and not to stop until it had killed all of them!

From the 14^{th} to the 18^{th} century, the Danish court, with the practical help of paid Dutch falconers, organized an effective trade of Gyrfalcons from Iceland and northern Scandinavia to Copenhagen (Oorschot 1974, Vaughan 1992, Christensen 1995). From 1664 to 1806, for example, more than 6,200 Gyrfalcons were exported from Iceland to Copenhagen. The number of exported falcons fluctuated considerably, with peaks in about every tenth year. This fluctuation most probably reflected population changes of ptarmigan, the main prey of the falcons (Nielsen and Pétursson 1995), these being the oldest published statistics known to ecologists to indicate cyclic predator-prey interactions.

The almost absolute dependence of Gyrfalcons on ptarmigan is now widely known, but the idea was published previously in 1864 by Newton (1864–1907, Vol. I of 1864, p. 97) who reported that only one clutch was found by Lapps in West Finnmark in 1859: "They searched together all the nests in two neighborhoods, but all were empty save this. They thought that the reason why the Falcons had flown away was that there were no Grouse to be found, and so they could not get food, but must fly away." Johansen and Østlyngen (2011) transcribed the original note by the respective egg-dealer Fredrik Wilhelm Knoblock. Actually, the famous Finnish bird artist and ornithologist Wilhelm von Wright, who drew and published the first naturalistic painting of the Scandinavian Gyrfalcon in 1832, seemed to understand the same fact decades earlier. In his diary from 12 August 1832, the day when the model female of his painting was shot while hunting a Hooded Crow (*Corvus corone*), von Wright wrote: "For a Gyrfalcon to be hunting a Crow, the ptarmigan population must be very small" (Leikola et al. 2008, p. 182).

In addition to falconers, egg-collectors also valued Gyrfalcons over most other northern birds in the early decades of Nordic ornithological history (e.g., Newton 1864–1907). In northern Fennoscandia, i.e., Norway, Sweden, Finland and Kola Peninsula, in the late 19th and early 20th Century, hundreds of falcon clutches were taken by tens of collectors, who employed local people for intensive "egg-hunting" of all northern birds (e.g., Wibeck 1960).

Long-lasting and large-scale egg-collecting, as well as trapping and shooting of adults as predators of economically valuable Rock Ptarmigan (*Lagopus muta*) and Willow Ptarmigan (*Lagopus lagopus*), were thought to have caused a population decline of the Gyrfalcon in northern Fennoscandia from the late 19th Century to the early 20th Century (Rassi et al. 1985, Koskimies 1989, Koskimies and Kohanov 1998, Väisänen et al. 1998). Because both egg-collecting and trapping virtually ceased 70–80 years ago, however, one may doubt whether these actions could have any long-lasting effect on the present population level (e.g., Cade et al. 1998, Koskimies 2006a). Tømmeraas (1993, 1994, 1998) and Holmberg and Falkdalen (1996) proposed that ptarmigan densities have declined to such critically low levels that Gyrfalcons cannot survive and reproduce properly. In Finland, however, practically all of the territories known from the 19th and 20th Centuries have been occupied during the last decade, in addition to an even larger number of newly-found territories (Koskimies 2006a, Mela and Koskimies 2006, Koskimies and Ollila 2009). In addition, only a few cliffs seemingly suitable for the Gyrfalcon have remained unoccupied during the last few years. Thus, there is no proof to the claim that the average level of the present Gyrfalcon population is only a fraction of that of 100–150 years ago (Koskimies 2006a).

Northern Fennoscandia is actually one of the very few areas within the Gyrfalcon's range where we are able to estimate the population size and density of the species since the mid-1850s (Tømmeraas 1993, 1994, Koskimies 2006a, Johansen and Østlyngen 2011). Because Gyrfalcons nowadays live there in closer proximity to human habitation and suffer from more human activities than in most other parts of the North, we have here a good situation for studying the versatile Gyrfalcon-human relationship both during a long and short time period (Koskimies 2006a). Thanks to national monitoring projects and a good basic knowledge of both the Gyrfalcon and its prey populations, especially in Finland (Koskimies and Väisänen 1991, Väisänen et al. 1998), we have been able to evaluate the status of and threats to the Gyrfalcon. Indeed, over a decade ago, this knowledge was essential for the compilation of an Action Plan as a guide-

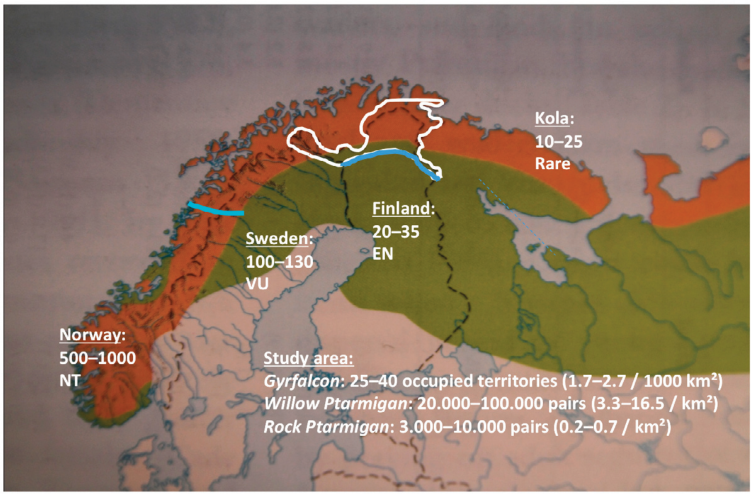


Figure 1. The Gyrfalcon's breeding (orange) and non-breeding distribution (green) in Fennoscandia according to Snow and Perrins (1998). In fact, the breeding range extends further south, up to the blue line from Sweden to Kola Peninsula (the total population from Norway to Kola, north of the blue boundary, is at least 330 pairs according to Koskimies 2006a). The area of the present study is shown by white boundaries. The estimated breeding population (pairs) and the status of the Gyrfalcon are shown by country (NT = Near Threatened, VU = Vulnerable, EN = Endangered). Population estimates (nesting pairs) of the Gyrfalcon, Willow Ptarmigan, and Rock Ptarmigan, as well as their densities in the study area, are listed separately.

line for practical conservation measures of the Gyrfalcon population in northern Europe (Koskimies 1999, 2006b).

In this article I summarize the results of my field research on the population dynamics of the Gyrfalcon in Finland and neighboring areas in northern Fennoscandia. I show how important it is to monitor an area large enough and a time period long enough to get reliable results on short- and long-term fluctuations of population size and productivity. In addition, I will briefly discuss the main threats to, and conservation measures for, the Fennoscandian Gyrfalcon population. My results and conclusions may help in the planning of monitoring and conservation in such parts of the species' range where surveys are just beginning.

By living in remote areas of wilderness, far from human habitation, the Gyrfalcon has thus far avoided many disturbance factors and threats by humans. It lives throughout the year in a more natural environment than almost any raptor species, having been fairly safe from direct disturbance, habitat change, or indirect factors like environmental pesticides. This apparent security of the Gyrfalcon, indicated also by the classification of the species as not threatened on a global scale (BirdLife International 2004), will likely change in response to climate warming.

Study Area and Methods

Study Area.—The study area lies in northern Finland and in the neighboring regions of northernmost Sweden and Norway (about 68–70° N and 20–30° E, Figure 1). This region, called Fell-Lapland in Finland, is relatively flat with gently sloping fell-mountains, the highest tops reaching ca. 1,000 m above sea level. The majority of the low-level country and wide valleys between fells, as well as lower fell slopes especially in eastern Lapland, are covered by barren pine-dominated forests (Scotch Pine, *Pinus sylvestris*); the higher slopes there and also the lower altitudes in western and northern parts of the area are dominated by low mountain birch forests (*Betula pubescens* ssp. *tortuosa*). Boggy and wet areas in most parts of the area are fairly small and bushy, with a thin turf layer compared to more extensive and wetter peatlands further south in Lapland. Small and medium-sized lakes abound.

Mapping and Surveying Nest Sites.—In my study area Gyrfalcons breed on cliff faces, almost always in twig nests built by Ravens (*Corvus corax*). Occasionally, some pairs accept old twig nests of the Rough-legged Buzzard (*Buteo lagopus*) or Golden Eagle (*Aquila chrysaetos*). A few pairs, in addition, nest every year in twig nests in trees, especially in northeastern Lapland (1–3 pairs have been found annually, and according to records of stationary birds and their distance from known nest sites, at least 1–2 more pairs nesting in trees may have remained unnoticed). In some territories, pairs have nested on cliffs and in trees in consecutive years.

In the early 1990s, I began mapping Finnish Gyrfalcon nest sites by collecting data from ornithological archives and other sources (Koskimies 2006a). During the 1990s and early 2000s, I visited previously known nest sites, most of them annually. I also looked for potential new nest sites by visiting over 200 cliff faces in total during that decade, classifying the suitability of almost all of them, and the availability of twig nests. At the end of the 1990s, Metsähallitus, the responsible governmental agency for conservation and monitoring of threatened animals and plants in state-owned lands in Lapland, also began mapping Gyrfalcon nest sites for practical conservation purposes (Mela and Koskimies 2006). Every year since the early 2000s, I have personally checked some 80–90% of the Gyrfalcon territories (both regularly and irregularly occupied) both in late winter (just before egg-laying or during early incubation) and in summer (during late nestling period). The remaining occupied territories were surveyed by 2–3 experienced field workers of Metsähallitus with similar methods and accuracy. During the last 10 years, relatively few nesting pairs, mainly in trees, have likely remained unnoticed in Finland, so the figures in this article on pair numbers and breeding success reflect true population fluctuations (see also Koskimies and Ollila 2009). Throughout the years, bird watchers, reindeer herders, hunters, hikers and other persons have submitted a number of observations which have been helpful to us in looking for alternative nest sites and previously unknown territories. In a way, these records act as a control for the coverage and accuracy of our monitoring project.

Since 2000, I have also systematically surveyed northernmost Sweden (Rostonselkä north of the River Lainio–Lake Råstojavri) and northeastern Norway (eastern Finnmark) close to the Finnish border; these areas were not covered by Swedish and Norwegian monitoring projects (Figure 1; for national Gyrfalcon monitoring projects in the Nordic countries, see Koskimies 1999, 2006a, 2006b, Johnsen 2004, Falkdalen et al. 2005). As in Finland, I had probably found all the occupied territories in these Swedish and Norwegian areas by the late 2000s.

In 1990–1993, I knew and checked only a few nest sites, all of them in June, 1–3 weeks before the young fledged. Since 1994, I have looked for and checked nest sites also in late March or April, when both breeding and non-breeding territorial pairs or lone birds were most probably at nest sites, or when signs of their presence were to be found. Since the late 1990s, a great number of nest sites have also been visited in August–November to collect prey remains and to look for suitable cliffs previously unchecked, as well as in mid-winter (January–February) to study winter ecology of the Gyrfalcon.

Field Methods.—Falcons visit their nest sites throughout the year. In addition to direct observations of falcons, occupied territories can be noted from signs left by birds. As I travelled to nest sites by skiing and walking from the nearest road, I also observed birds away from nest sites. Adults were photographed and in many cases filmed on video, and their behavior and appearance recorded for individual recognition. Molted feathers were collected at nest sites since 1997.

In most years since the end of the 1990s, the majority of known and regularly occupied nest sites have been visited several times a year, first (typically) in January or February to check for winter occupancy. All territories, occupied at least once during the study years, have been checked in late March or in April, during or just before egg-laying or early incubation, to confirm the number of pairs starting to breed and the number of other territorial birds. Territories occupied in late winter or spring were rechecked in mid- or late June to count the number of big nestlings (as suggested by Postupalsky 1974).

In March and April, nests were checked at a distance by binoculars or telescopes to avoid disturbance of the falcons. The most regularly occupied nest sites in a given territory were checked first, and if neither birds nor signs of their presence were observed, alternative nest sites were visited. At every site, feathers, feces, prey remains, tracks in snow, and signs of recent presence of falcons were carefully sought.

During the June visit the young were usually 5–8 weeks old, and all of them would likely fledge. If climbing could be brief and cause little disturbance to the birds, the nestlings were ringed with standard rings, and in many years in the late 1990s and early 2000s also with special colored metal rings, the codes of which could be read with telescopes or from photographs. Prey remains were collected at nest sites since 1998 (Koskimies and Sulkava 2011). In addition to traces of falcons, any hints of visits by people at nest sites were recorded to estimate possible disturbance to breeding success. In many years a substantial number of occupied territories were surveyed from late August to November to collect prey remains from the late nestling and fledgling period, and to record if the birds remained at nest sites during that time of the year.

Monitoring of Ptarmigan.—Every Willow and Rock Ptarmigan seen or heard while skiing and walking along the standard routes to and from nests sites of the Gyrfalcon have been recorded since the beginning of the Gyrfalcon study. The Willow Ptarmigan is the most important prey for falcons in my study area, and its population density in late winter and early spring is probably critically influential upon the reproductive potential of the Gyrfalcons (Koskimies and Sulkava 2011, see also Cade et al. 1998, Koskimies 2006a, Nielsen 2003). To indicate the availability of food for the falcons, I calculated an annual index of the Willow Ptarmigan population by comparing the number of birds observed in March and April during trips to the same nest sites in consecutive years. The total number of Willow Ptarmigan individuals in the year-to-year comparisons of the same routes varied from 13 to 151.

Results

Density Fluctuations of Willow Ptarmigan in Northern Lapland.—The Willow and Rock Ptarmigan are the most important prey of the Gyrfalcon in interior northern Fennoscandia: almost 90% of the prey items are ptarmigan during the breeding season, a time when there are also waders, waterfowl, gulls, terns, and other prey available (Koskimies and Sulkava 2011). In winter there are practically no other prey species available in such numbers that could play any significant role in food composition and energetics of the Gyrfalcon.

In my study area, about three quarters of the ptarmigan preyed upon by Gyrfalcons during the breeding season, i.e., from late winter to late summer, were Willow Ptarmigan. The Willow Ptarmigan is the only prey available in sufficient abundance to allow most Gyrfalcons to survive over winter and begin breeding. Thus, the abundance of Willow Ptarmigan has a critical effect on the viability of the Gyrfalcon population. In some territories, Rock Ptarmigan form a substantial part of the diet (Koskimies and Sulkava 2011), but generally, in my study area, the Gyrfalcon population is absolutely dependent on the abundance of Willow Ptarmigan for survival and reproduction.

The density of Willow Ptarmigan varied nine-fold during 2000–2010 in my study area during late winter and early spring, with highest densities in 2003–2006, whereas only a fraction existed in 2007–2010 (Figure 2). According to game bird monitoring by the Fisheries and Game Research Institute, Willow Ptarmigan population density in August in the mid-2000s was higher than at any time since the early 1960s when annual and comparable monitoring censuses began (e.g., Väisänen et al. 1998, Helle and Wikman 2005, 2006). Similarly, during 2008–2010, the density crashed to the minimum ever recorded since the 1960s (Wikman 2010), and it is noteworthy that the extremely low densities simultaneously extended further away from Finland than normally, at least to the Kola Peninsula to the east and Central Scandinavia to the west (Koskimies unpubl. obs.).

Game censuses monitored Willow Ptarmigan density in August by counting both adult and juveniles along census routes 60 m wide (Lindén et al. 1996). A single route is a 12-km-long equilateral triangle (3x4 km) situated randomly in the landscape. These game censuses have been made throughout Lapland, whereas my census area is limited to the northern third of that area. Willow Ptarmigan populations in various parts of Lapland, however, have fluctuated similarly during recent decades (e.g., Väisänen et al. 1998). The game census results are not directly comparable with my censuses along the routes to and from Gyrfalcon nests for many other reasons, most obviously because of differences in observability of the birds in late winter compared to August, e.g., differences in flocking, vocalizations, other behavioral traits, as well as weather, vegetation, and other factors. Despite this, both my indices from late winter and early spring, and the game census indices from August, have fluctuated in the same manner and synchrony from year to year during the last 11 years (Figure 2). My indices most probably reflect real density fluctuations in the study area.

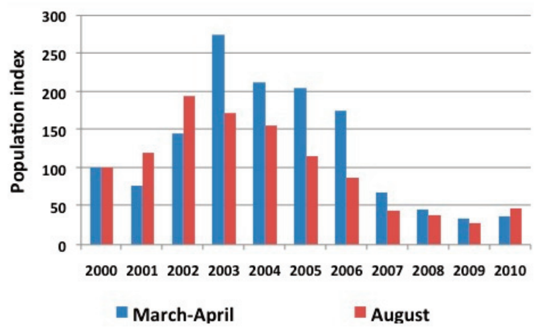


Figure 2. Population fluctuations of the Willow Ptarmigan in northern Fennoscandia from 2000 to 2010 in late winter (late March and April, 100 = 1.0 individuals/sq.km), and in August (100 = 3.2 individuals per/km²).

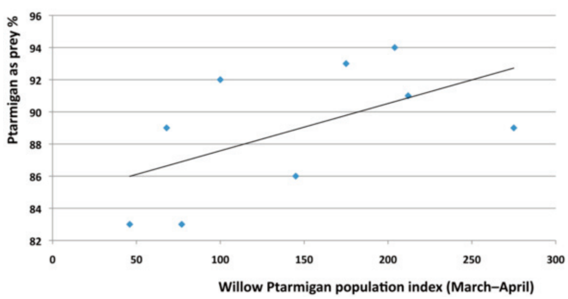
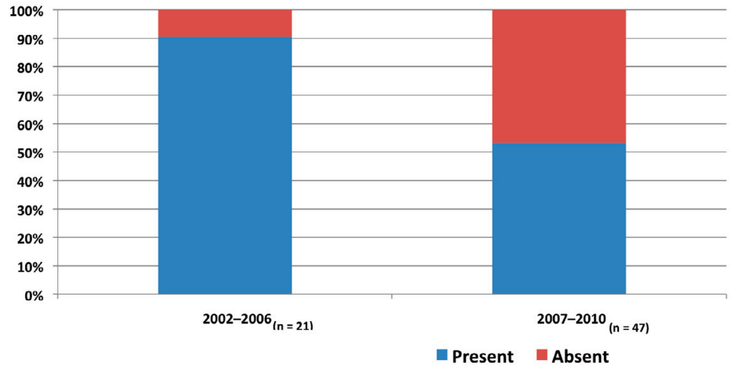


Figure 3. The percentage of Willow and Rock Ptarmigan among the total number of prey individuals in the Gyrfalcon diet in northern Fennoscandia according to the relative density of the Willow Ptarmigan in late winter (see Figure 2).

The importance of ptarmigan, and especially Willow Ptarmigan, in the diet of the Gyrfalcon is reflected also by the fact that the percentage of ptarmigan of all prey items grew by 3–4% in 2003–2006 compared to earlier and later years when their density in the field was only one-quarter to one-third of that maximum period (Koskimies and Sulkava 2011, Figure 3).

Structure of Gyrfalcon Population and Territorial Behavior.—The Gyrfalcon population consists of breeding pairs, non-breeding terri-

Figure 4. The presence of Gyrfalcons at their nest sites in mid-winter (in late January or in February) during two periods with different relative densities of Willow Ptarmigan in late winter (average WP index in 2002–2006 202, in 2007–2010 46, respectively; see Figure 2).



torial pairs, and lone territorial birds, as well as non-territorial individuals. I have monitored the number of territorial birds by checking potential habitats and suitable nest sites throughout the year. I have not been able to estimate the size of the floating population because of lack of suitable methods (see also Booms et al. 2008).

Territorial Gyrfalcons visit their nest sites throughout the year in my study area based on direct observations and signs of their presence. In addition to late winter and early spring, I have seen territorial and courtship behavior several times in autumn and early winter, and even in late November. Several times I have seen the female begging for food from her mate during the last week of January and first two weeks of February, 2–2.5 months before egg-laying. On few occasions, I have seen Gyrfalcons copulating weeks before egg-laying.

Many pairs or lone territory-holding birds stay on nesting cliffs, typically within 10–300 m of nest sites, during mid-winter. They prefer to roost and rest during daytime on those cliffs that are most protected from wind and snowfall. Thick layers of whitewash indicate the most popular sites. Some of the birds were probably away for weeks at a time, as in most cases, they were absent during my short (typically 1–2 hour) visits, and many times there were no fresh signs since the last snowfall.

Effect of Ptarmigan Density on Winter Occupancy of Nest Sites.—I visited Gyrfalcon territories in mid-winter (from late January to mid-February) for several years, and checked all suitable nest sites within these territories. From 2002 to 2006, I surveyed the nest sites of 14 different territories 21 times in total, and from 2007 to 2010 mostly these same territories 47 times (one time = one separate winter period). The presence of falcons at or near nesting cliffs was determined by fresh droppings, feathers, and other signs, and sometimes by direct observations of birds.

During the first period (2002–2006), late winter density of Willow Ptarmigan was 3–9 times as high as during the second period (2007–2010, Figure 4). Also the occupancy rate of the nesting cliffs by Gyrfalcons varied markedly between these two periods: during the first period, Gyrfalcons were, or had recently been, present in 90% of the territories surveyed, while during the second period, I could record their presence only in half of the cases. Most probably, the high Willow Ptarmigan density during the first period made it possible for almost all falcons to overwinter at their nest sites.

Nesting Frequency of Gyrfalcons by Territory.—As I have been able to monitor practically all Gyrfalcon territories in my study area in Finland and in nearby neighborhoods of Sweden and Norway in recent years, it is possible to analyze in more detail the occupation rate of individual territories. The rate of occupation by Gyrfalcons varied greatly both from territory to territory and within a territory from year to year (Figure 5). Of the 59 territories checked at least once during the study period since 1990, three remained without a single nesting attempt during the study period. One of these was occupied by a non-breeding pair or a lone bird during one of three years surveyed, one during two of eight, and one during two of nine years (Figure 5).

All the other 56 territories hosted a breeding pair at least once, but the frequency of years with a breeding pair varied markedly from territory to territory. Half of the territories had a breeding pair, on average, every third year or less often (Figure 6). Because the majority of the territories were unknown to me during the 1990s (Figure 5), I compared the occupation rate of breeding pairs from 2000 to 2010 when practically all of the territories were known, and almost all of them were checked at least two times yearly (in late March or April and in June). Of the 25 territories that were surveyed every year during this 11-year period, half (12) had a breeding pair in every second year or more often (at least 5 years of the 11, in total; Figure 7). One quarter of the territories were occupied only once or twice during the 11 years. The median rate of territory occupancy by a breeding pair was four in 11 years. This period, however, being the first 11 years of the 21st Century, were abnormal for the Fennoscandian Gyrfalcon population because the density of Willow Ptarmigan was higher around 2003–2006 than during several decades previously, while after that, it crashed to the lowest level since the 1960s. Although breeding pairs most often refrained from breeding in consecutive years (in almost half of the cases), there were some territories where falcons nested up to 7–8 consecutive years or even longer (Figures 5, 7).

The territories in Enontekiö and West Inari, western Lapland, seem to have been occupied slightly less often and for shorter periods in succession than in Utsjoki and East Inari in northern Lapland. Figure 5 shows also that closely neighboring territories were, in many parts of my study area, occupied somewhat more synchronously than those more widely spaced. The general norm was that, if a territory was occupied by Gyrfalcons, they nested or remained there non-breeding at least two years in succession (Figure 5) before the territory became unoccupied. In general, it was typical for a breeding pair to nest only once, after which the birds remained non-breeding the following year in their territory. It was much less common for a Gyrfalcon pair to nest during several consecutive years (Figure 8).

Effect of Willow Ptarmigan Density on the Percentage of Breeding Pairs.—The number of breeding pairs and non-breeding territorial Gyrfalcons increased in my study area during the first years of the 21st Century (see also Koskimies and Ollila 2009). Because a substantial number of territories were not found prior to those years, however, I cannot say how many of them were occupied by Gyrfalcons 10–20 years earlier. But I can compare the occupation rate by breeding pairs and non-breeding territorial birds of all the territories surveyed from 2000 to 2010. The percentage of territories occupied by breeding pairs increased from 30–40% to 50–55% during the five years from 2002 to 2007 when Willow Ptarmigan density increased threefold and then receded to the original level (Figure 9). The maximum proportion of breeding pairs was reached four years after the ptarmigan peak, although ptarmigan density remained high for two more years after the peak (Figure 3, 9). Thus, the time lag from the population high of Willow Ptarmigan to that of the Gyrfalcon was two years.

In 2009–2010, only about one-tenth of the territories had a breeding falcon pair, and a markedly greater percentage (30–40%) of territorial falcons refrained from breeding compared to most years (10–25% of the territories surveyed were occupied by non-breeding birds). Thus, the number of breeding pairs varies with larger amplitude than the size of the total population. For a nine-fold difference in the density of Willow Ptarmigan, the per-

Figure 5. Occupation by breeding and non-breeding Gyrfalcons in the 59 nesting territories in the study area from 1990 to 2010 (green = breeding pair, orange = non-breeding territorial pair or lone falcon, blue = unoccupied, white = not surveyed). The territories are listed from west to east and northeast so that neighboring territories are listed consecutively. The figures indicate the number of large nestlings (probably fledging; 0 = unsuccessful nesting attempt, ? = successful nesting but number of nestlings unknown).

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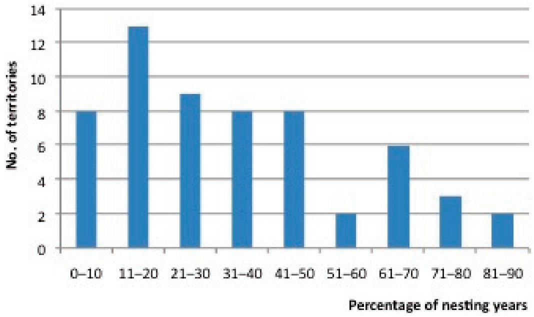

Figure 6. The number of territories in northern Fennoscandia according to the percentage of years occupied by breeding Gyrfalcons in all the years they were surveyed from 1990 to 2010. Note that not all territories were surveyed annually before the early 2000s (see Figure 5).

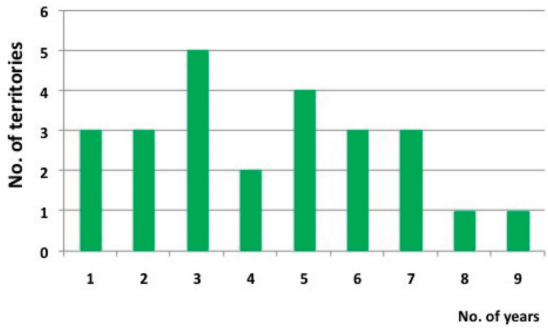

Figure 7. The number of annually surveyed territories in northern Fennoscandia according to the number of years occupied by breeding Gyrfalcons from 2000 to 2010 (see Figure 5).

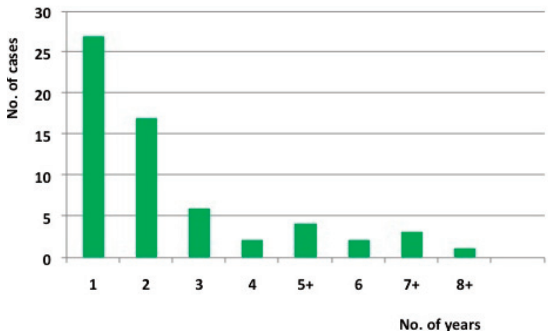

Figure 8. The number of nesting attempts in the annually surveyed territories in northern Fennoscandia according to the number of consecutive years occupied by breeding Gyrfalcons from 2000 to 2010 (see Figure 5).

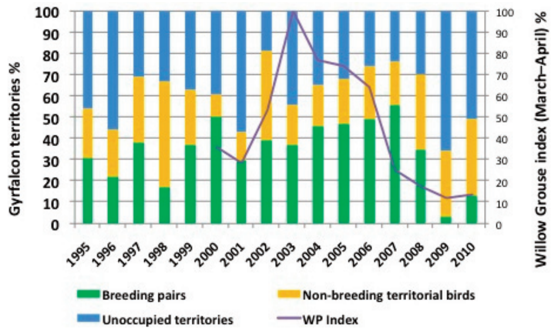

Figure 9. The percentage of territories occupied by breeding pairs and non-breeding Gyrfalcons in the territories surveyed in northern Fennoscandia from 1995 to 2010, and the percentage of the Willow Ptarmigan density index in late winter of the maximum (2003) figure (see Figure 2). Note that all territories of the study area were not surveyed annually before the early 2000s (see Figure 5).

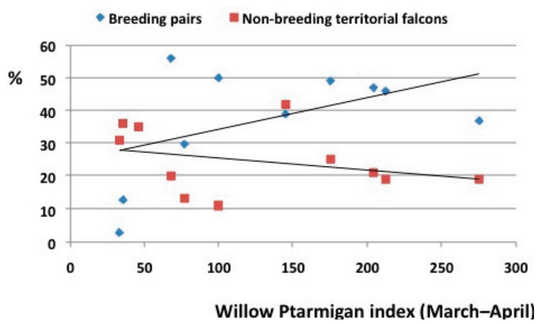

Figure 10. The percentage of territories occupied by breeding pairs and non-breeding territorial Gyrfalcons according to the relative density of the Willow Ptarmigan in late winter from 2000 to 2010 (see Figure 2).

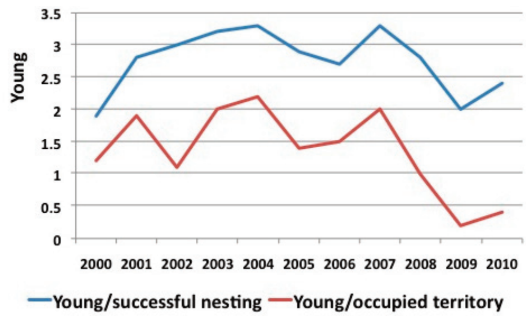

Figure 11. The average number of large nestlings (probably fledging) per successfully nesting pair, and per number of territories occupied by Gyrfalcons in northern Fennoscandia from 2000 to 2010.

centage of territories with a breeding pair varied about at the same amplitude while the percentage of all territories occupied by Gyrfalcons only halved from the peak to the bottom year of the ptarmigan density (Figure 9). Neither the percentage of breeding pairs nor that of non-breeding territorial birds, however, fluctuated linearly with ptarmigan density, as they seemed to have already reached the final levels when ptarmigan density was no higher than one-third of its maximum (Figure 10). During my most intensive study period (11 years), this has happened in about two years in three, on average.

Breeding Success of the Gyrfalcon.—From 1990 to 2010, Gyrfalcon territories were surveyed 619 times in my study area (the annual sums of surveyed territories counted together). Pairs started to nest 214 times, i.e., 34.6%. Of these nesting attempts, 36 (17%) appeared to fail during the egg-stage, and only four (2%) after hatching. Thus, 81% of the pairs that laid eggs were successful in raising at least one young. Two broods were killed by Golden Eagles, and a few young (and once a whole brood of four) fell from nests. Some clutches were deserted, and several were destroyed by unknown causes. Raven pairs commonly nested within some hundreds of meters of Gyrfalcon nests, and these two species often quarreled with each other, which may in some instances have led to failure of one or the other of them. Once a pair of the Peregrine Falcons (*Falco peregrinus*) nested only 22 m from a Gyrfalcon nest, and the two falcon species fought heavily at least up to the late nestling period. On that occasion, the Gyrfalcons raised three young while the Peregrines lost their young early in the nestling period for unknown reasons.

The number of young per brood varied from one to five during 1990–2010, with 2.93 young per successful pair, on average (2.98 in the main study period 2000–2010). The number of young per occupied territory was 1.40 during the entire study, and 1.34 during the main study period (2000–2010), with most of the territories included annually (see Figure 5). Among successful nests, the most common brood size in my whole data set (1990–2010) has been three (59 cases of 167, or 35%), followed by broods of four (54, 32%), and then two (42, 25%). One-young broods were observed only 11 times (7%) and five young (all within a week of fledging) only once (Koskimies 2004). Broods of five young are very exceptional; Potapov and Sale (2005) examined published data on hundreds of clutches and broods throughout the species' range, and although two percent of the clutches

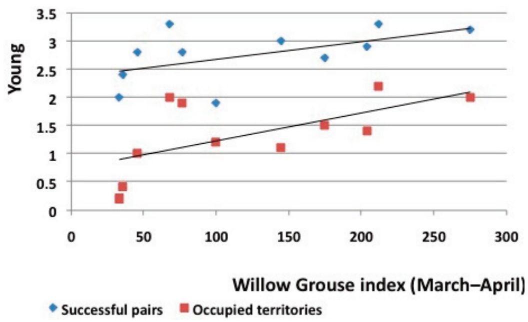

Figure 12. The average number of large nestlings (probably fledging) per successfully nesting pairs, and per number of territories occupied by Gyrfalcons in northern Fennoscandia from 2000 to 2010 according to the relative density of the Willow Ptarmigan in late winter (see Figure 2).

had five eggs, they reported not a single brood of five young, although they refer to Bengtson (1972) from Iceland who found two broods with five young (in one of them all five fledged). In the literature, in addition to Bengtson (1972) and my own case, I have found a reference to five young in a brood only twice: in Central Norway in 2003 (Tømmeraas 2003), and on the Yamal peninsula in northern Russia in 2007 (Mechnikova and Kudryavtsev 2007).

I analyzed the effect of Willow Ptarmigan population density on the breeding success of the Gyrfalcon from 2000 to 2010, the years with all or most of the territories surveyed, and with a sufficient number of ptarmigan counted in March–April. The number of young per successful pair varied from 2.0 to 3.3, and the number of young per occupied territory from 0.2 to 2.2, respectively (Figure 11).

Although I have not yet determined if the habitat of the nest site, or the type of nest, or any other measurable character of the territory, may have any effect on the breeding success of the Gyrfalcon, it seems clear that the population density of Willow Ptarmigan is the primary causal factor (Figure 12). Both the number of Gyrfalcon young per occupied territory (the total territorial population), and the number of young per successful pair, varied in synchrony during 2000 to 2010 and reflected changes in the ptarmigan population. During 2000–2002, when the ptarmigan population was increasing at the average level of recent decades, the mean annual number of Gyrfalcon young per occupied territory varied from 1.1 to 1.7, and that of successful pairs from 2.7 to 3.0. Both figures reached their peaks (2.2 per occupied territory and 3.3 per successful pair) in 2004, one year after the maximum density of Willow Ptarmigan. After a slight decline in 2005–2006, they rose once more in 2007, although the ptarmigan density had declined to one-third of its value from 2004.

A plausible explanation for the delayed decline of breeding success years after the Willow Ptarmigan peak may be that the density of Rock Ptarmigan, which probably varies less from year to year than that of Willow Ptarmigan (e.g., Väisänen et al. 1998, Pedersen and Karlsen 2007), remained at a fairly high level, at least up to 2007. Although I have no data on annual population changes of Rock Ptarmigan, this explanation can be roughly evaluated by comparing the percentages of ptarmigan species in Gyrfalcon prey remains. The proportion of Rock Ptarmigan was highest in 2005 (39.6% of total *Lagopus* spp.), 2004 (35.0%), and 2002 (36.2%, Koskimies and Sulkava unpublished). In 2006, it dropped to 14.5%, but increased once more to 25.2% in 2007, before dropping to 2.3% in 2008. Thus, there is some support for the idea that, in addition to Willow Ptarmigan, optimal territories and pairs should have fairly easy access to Rock Ptarmigan, as suggested by the fairly regular occupation of those territories where higher-than-average proportions of Rock Ptarmigan were noted in the diet (Koskimies and Sulkava 2011). The limited and random information on the abundance of Rock Ptarmigan in 2008–2010 suggests that both species of ptarmigan declined considerably after 2007 in my study area.

During the period of exceptionally low density of Willow Ptarmigan in 2009–2010 (Figure 2), the mean number of Gyrfalcon young in successful nests remained fairly high (2.0 and 2.4 per brood among only seven broods in total during the two years, Figure 11). The number of young per occupied territory, however, was exceptionally low, only 0.2–0.4, because the majority of territorial birds did not produce any young at all. Thus, while Willow Ptarmigan density varied nine-fold from bottom to top in 2000–2010, the number of young Gyrfalcons per occupied territory varied about four-fold, whereas the annual number of young per successful pair varied only by 1.5-fold (Figures 11, 12).

Annual Fluctuations of Population Size and Breeding Success in Sweden.—To confirm the generality of my findings on the nature and amplitude of the annual fluctuations of breeding success, as well as of population size of the Gyrfalcon in other parts of northern Fennoscandia, I compared them with the published results available from Sweden during the last decade (e.g., Falkdalen et al. 2005, Ekenstedt 2006, 2008, Ekenstedt and Johansson 2009, Tjernberg 2010; see Figures 13 and 14). The Swedish studies from Jämtland-Härjedalen, western Sweden close to the Norwegian border on the Scandinavian mountains, to Norrbotten and Västerbotten, North Sweden, cover over half of the national range and population. The territories have been surveyed and the young counted by comparable methods with those used in my study area in Finland and the bordering areas. The main study area in Norrbotten consists of two sub-areas: National Parks (Sarek, Padjelanta and Stora Sjöfallet), being protected and with restricted human activity (no ptarmigan hunting), and Kirunafjällen, without conservation areas and ptarmigan hunting allowed (e.g., Ekenstedt 2008).

Although there are some differences in timing of the peaks and lows of both the number of breeding pairs and the number of young per occupied territory, very probably reflecting the spatial and temporal variability of prey densities, the general pattern of annual fluctuations in the number of occupied territories (Figure 13) and breeding success (Figure 14) remain quite similar. One reason for the temporal differences between Finland, and especially Jämtland-Härjedalen and Norrbotten, must be that the Rock Ptarmigan is the dominant prey in a greater proportion of territories in the latter areas, situated at or close to the Scandinavian high mountains (Nyström 2005, Nyström et al. 2005). The Finnish and Swedish figures may also be compared with the Norwegian results of Johansen and Østlyngen (2011) from a smaller study area further north in western Finnmark; they show similar variation both in the number of pairs and breeding success, but, as in the other areas, with temporal, region-specific peculiarities.

Nest Site and Mate Fidelity, and Number of Years Present in a Territory.—I have not had resources to properly analyze my material (especially DNA from shed feathers) on nest site and mate fidelity and on population turnover of Gyrfalcons thus far. After visiting about 200 active nests and other occupied territories, most of them more than once per year, and after looking carefully for differences in plumage and behavior of the adults, both in the field and on photographs, I have the impression that both sexes are very faithful to their nest sites of the previous year. At many nest sites, one or both of the adults have remained the same for years, even in cases where there has been a year or a few years without nesting. In some other territories, adults have been replaced within only a year or two. I found two dead Gyrfalcon females in my study area, one of which was killed on its nest by a Golden Eagle.

According to my preliminary analyses, based on the field notes on the plumage and behavior of Gyrfalcon females—for example, their aggressiveness or shyness towards human, overflying activity, noisiness, peculiar voices, preferred perch sites, etc.—I have compiled the

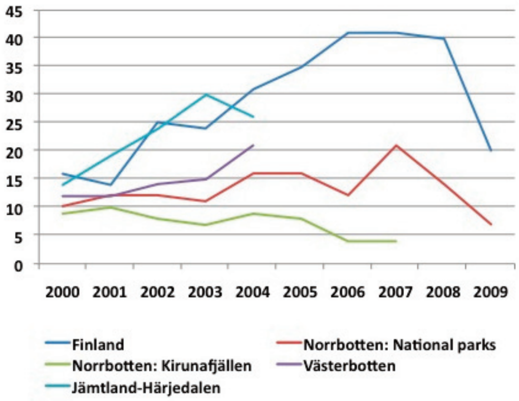

Figure 13. The number of Gyrfalcon pairs (Norrbotten) and the number of occupied territories (pairs and lone birds, other study areas) in Finland (this study) and Sweden in 2000–2009, from years with published information (for references, see text). In 2009, there were eight occupied territories in Västerbotten and 22 in Jämtland-Härjedalen. Note that the number of controlled territories (study effort) has varied somewhat annually especially in Finland and Västerbotten during the first years of the decade (see text).

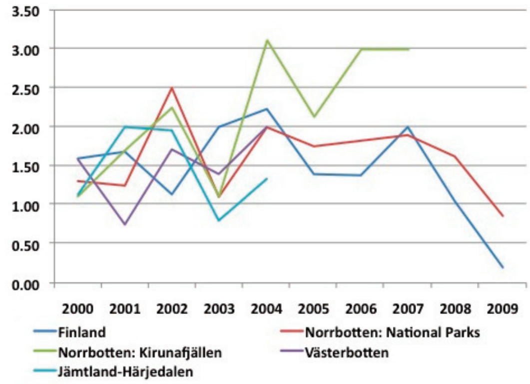

Figure 14. The average number of large nestlings (probably fledging) per pair (Norrbotten) and per occupied territory (other study areas) in Finland (this study) and Sweden in 2000–2009, from years with published information (for references, see text). In 2009, the figures were 2.40 in Västerbotten and 0.91 in Jämtland-Härjedalen.

following statistics, dividing the individuals into two classes. First, from 27 territories, I identified 32 different females of which both the first and last year of breeding or occupation were known (I surveyed the territory in years both before and after the bird was observed for the first and last time). Second, I identified 22 additional, different females that occupied their territories from the first to the last year of my surveys (usually 2010), so they may have remained there for more years than recorded.

I took into account only those females for which I had good grounds to believe they were the same from year to year. They included one bird which surely moved from one territory to a neighboring one and continued nesting there, but in all other cases they were recorded within only one territory. My results are surely not as accurate and valid as one could get from ringing, but as Gyrfalcons are difficult to trap, and because trapping is disturbing to the birds, a better option for conservation purposes is to use non-invasive methods with less-than-perfect accuracy. I plan to check these statistics by DNA-analyses of shed feathers, also a non-invasive but more accurate method for individual identification of birds. This preliminary interpretation without DNA-analyses suggests that the mean number of years for a female to occupy a territory is three years.

Table 1 lists, as noted above, only females because a large proportion of males were not observed; they spend much time hunting away from nest sites. According to a small number of identified males, their tenure seems as variable as that of the females. At least one male occupied a territory for eight or more years.

Population Size of the Gyrfalcon in Fennoscandia.—According to a total count, there were 59 territories occupied by Gyrfalcons at least once in my study area since the

Table 1. The number of females in different time periods of territory occupation: the first set of data with the first and last year of occupation possibly known, the second set with additional individuals with less precise survey accuracy (see text on the previous page).

No. of years	No. of females	No. of years	No. of females
1	10	> 1	3
2	4	> 2	2
3	8	> 3	6
4	3	> 4	1
5	4	> 5	3
6	2	> 5	5
8	1	> 8	2

early 1990s. A breeding pair was noted at least once at 56 territories, and only non-breeding individuals at three other territories (Figure 5). The best years were 2006 (55 territories surveyed, of which 27 had a breeding pair and 14 were occupied by non-breeding individuals), and 2007 (54 surveyed, of which 30 had breeding pairs and 11 had non-breeders). The worst year was 2009 (58 surveyed, of which two contained a breeding pair and 18 had non-breeders, all the rest unoccupied). In most years there seem to be 25–40 occupied territories in my study area, which means ca. 1.7–2.7 territories per 1,000 km^2.

There are other intensive monitoring projects on Gyrfalcons going on in Scandinavia and the Kola Peninsula (e.g., Koskimies 1999, 2006a, 2006b, Steen 1999, Johnsen 2004, Johansen and Østlyngen 2011, Falkdalen et al. 2005, Ekenstedt 2006, Tjernberg 2010, Lindberg et al. 2010, Ganusevich 1992, 2001, unpubl.). In Norway, those surveys covered only minor regions in various parts of the country at present, while in Sweden, studies included about two thirds of the breeding range and the total national population, with a good and representative spatial and temporal sample. In Kola, most of the potential territories are annually checked nowadays, with a long-term monitoring especially along the River Ponoy valley in the central parts of the peninsula (Ganusevich 1992).

By extrapolating from regional data, the Norwegian population is now estimated, a little surprisingly, at as many as 500–1,000 pairs ("1,000–2,000 reproductive individuals") by Artsdatabanken (2010), the governmental administrative organization responsible for the classification of the threatened species (by expert group, Kålås et al. 2011). Recent earlier estimates were only about 300–500 breeding pairs (e.g., Steen 1999, Koskimies 1999, 2006a, 2006b, BirdLife International 2004). The Swedish estimate has remained at the present order of magnitude, 100–130 breeding pairs, for decades, without any trends at least since the early 20th Century (Lindberg et al. 2010, Koskimies 1999, 2006a, 2006b, BirdLife International 2004), as in Finland, too. According to the above mentioned national and other regional monitoring projects, no marked changes in population size have been documented in other parts of northern Fennoscandia in recent decades (Koskimies 1999, 2006a, 2006b, Koskimies and Ollila 2009).

On the Kola Peninsula, Ganusevich has visited a substantial number of known territories since the late 1970s, and in recent years he has checked as many of them as possible and intensively looked for new ones. In 2010, for example, Ganusevich (unpubl.) knew of 31 territories from previous years and checked 26 of them. Of these, 11 were occupied by Gyrfalcons, and four had a breeding pair. The number of breeding pairs in 2010 is most probably lower than average for this area because Willow Ptarmigan density was extremely low on the Kola Peninsula in 2010, as was the case in Finland and northern Scandinavia. Based on these figures and information from Koskimies and Kohanov (1998) as well as from Potapov and Sale (2005), I estimate that the present breeding population in Kola Peninsula may vary from 10 to 25 pairs in most years. Large parts of the Kola are covered by barren and rocky pine forests and pine peat bogs which explains the low average density for many other raptor species, too.

Thus, the total number of breeding Gyrfalcon pairs in Fennoscandia, including Norway, Sweden, Finland, and the Kola Peninsula, can be estimated at ca. 600–1,200 pairs, twice as many as thought less than a decade ago (Koskimies 2006a, 2006b). This is due to a marked increase in the Norwegian estimate which needs to be verified by more representative, intensive, and large-scale studies, both spatially and temporarily, in the near future.

DISCUSSION

The following discussion concentrates on factors that influence population dynamics of the Gyrfalcon, as well as the main threats and most promising conservation measures in northern Fennoscandia according to the Action Plan of the European Union (Koskimies 1999, 2006b), and is based on my personal experiences from long-term field studies. As the present population trend and long-term changes are also important for planning and evaluating aims and methods of future conservation, I summarize my earlier discussion (Koskimies 2006a) on what we know, and how we should interpret the evidence of population fluctuations of the Gyrfalcon in northern Fennoscandia since the mid-1800s (see also Johansen and Østlyngen 2011 for a critical analysis from a well-researched sub-area).

The Importance of Suitable Cliffs and Abundant Prey for the Gyrfalcon.—The two most critical environmental factors for a viable Gyrfalcon population are availability of suitable prey throughout the year and secure nest sites for breeding (see Koskimies 1999, 2006b). In my study area in Finland and in the border areas of Sweden and Norway, the landscape is rather flat, and abrupt cliffs are scarce in most parts of the area. Some 5–10 years ago, when new pairs had settled in my study area following record-high densities of Willow Ptarmigan and the consequent increased reproductive success of the Gyrfalcon, practically all suitable nest sites were occupied for several years. Especially in the eastern part of my study area, 1–3 pairs nested in trees, both in pines and birches, where old twig nests of the Raven and the Golden Eagle provided acceptable nesting possibilities in areas where there were no suitable cliff faces. These parts of my study area included large areas of habitat suitable for Willow Ptarmigan, and there some Gyrfalcon pairs annually demonstrated their flexibility in choosing abnormal nest sites.

Thus, availability of prey seems to act as the most critical determinant for the size, density, and breeding success of the Gyrfalcon population in northern Fennoscandia. The falcons seem to visit their territories more or less regularly in wintertime, probably to secure ownership of the nest sites which are in short supply. Especially in such a situation when there are more recruits than average, as in the mid-2000s, it is necessary for a territorial pair to guard its nest site throughout most of the year. It is probably a good strategy to remain stationary also because hunting should be more efficient for a raptor staying in a familiar area, especially for a Gyrfalcon which preys on ptarmigan almost the year round.

During the coldest and darkest months of the winter a Gyrfalcon has to protect itself from strong wind, snow storms, and other types of harsh weather, as well as from Golden Eagles which may sometimes kill falcons. It is beneficial for a falcon to know one or more safe roosting and resting sites, where the bird has to spend the great majority of the time, especially during the two months without any sunshine in North Lapland, and where temperatures may decline to -40ºC and even lower for several days or weeks. There are also other birds, like Ravens and Golden Eagles, which prefer similar roosting cliffs, so it is advantageous for a falcon to find a suitable place free of these rivals or predators. The requirements for a safe nesting site, as well as for a roosting and resting place during the non-breeding season are probably fairly similar, and thus it is in many ways beneficial for the Gyrfalcons to overwinter at or close to their familiar nest sites and hunting grounds.

In addition to requirements for nesting and roosting habitat, the Gyrfalcons are very highly specialized in their foraging ecology, mainly because there are so few suitable prey species available from early autumn to late spring in arctic and subarctic latitudes. In my study area, Willow Ptarmigan form two thirds, and Rock Ptarmigan about one quarter, of the diet during the breeding season, whereas other prey species, almost all of them migratory birds, form only about ten percent (Koskimies and Sulkava 2011). During the non-breeding season, only a fraction of alternative prey, like corvids, Black Grouse (*Tetrao tetrix*), and small passerines, are available, compared to summer.

Numbers of both ptarmigan species, and especially Willow Ptarmigan, fluctuate in a cyclical manner, with consecutive peaks and lows usually following after 3–5 years (e.g., Väisänen et al. 1998). As there are no other prey species in appropriate numbers available during winter and during the first weeks of the nesting period, ptarmigan density has a definite effect on the Gyrfalcons' reproduction and population dynamics. A certain density of Willow and Rock Ptarmigan must therefore be absolutely critical for the survival and nesting of the Gyrfalcon (e.g., Holmberg and Falkdalen 1996, Cade et al. 1998, Koskimies 1999, 2006b, Koskimies and Sulkava 2011).

For conservation purposes, it is very important to determine this threshold density of ptarmigan. The first decade of the 21st Century in my study area included a period when Willow Ptarmigan density varied from exceptionally low to record-high. Successfully breeding falcons were able to produce a fairly satisfactory number of young in all years except those with the lowest ptarmigan density, as compared to other studies (e.g., Cade et al. 1998, Nielsen 2003, Booms et al. 2008). According to my study, Gyrfalcons can manage more or less satisfactorily when the Willow Ptarmigan index counted by my method is at least one individual per km^2 at the beginning of the nesting season. An unknown portion of the ptarmigan present, however, may remain unrecorded when a man traverses on skis a mountain birch forest, the normal habitat of Willow Ptarmigan; thus, the next step should be to determine the real density of the ptarmigan relative to the index value I obtained while skiing. According to Wikman (2010), trained dogs found 1.2–1.9 times as many Willow Ptarmigan in northern Lapland in August 2008–2010 as three men using the standard Finnish method, i.e., walking side by side and covering a 60 m-wide transect. In late winter and early spring, however, the birds live in larger flocks and have a different probability of being detected.

The densities of Willow Ptarmigan and, to a lesser extent, Rock Ptarmigan in my study area most critically affect the percentage of territorial pairs which lay eggs, usually in late March or early April. As the male feeds the female in the weeks before egg-laying, it must be the female's physical condition and energetic resources to form eggs which ultimately determine the reproductive output of the season. The percentage of females laying eggs is the factor that responds most accurately to food availability, while the average number of young in successful nests fluctuates only 1.5-fold between peak and low years.

Gyrfalcons adapt to cyclically fluctuating ptarmigan densities by refraining from nesting when the prey population is below the critical threshold level, as shown, for example, by Nielsen (2003) in Iceland in a decades-long study, as well as by Potapov and Sale (2005) in their compilation of shorter-term studies from various parts of the species' range. The amplitude of variation of the Rock Ptarmigan population in Iceland has been 4.2, while that of the Gyrfalcon territorial population has been 1.5, and of the Gyrfalcon breeding population 3.6 (Cade et al. 1998). These original data by Ólafur K. Nielsen from 1981 to 1996 shows that, of the 804 observation years for occupied territories, 355 (44%) had no sign of breeding, 72 (9%) had failed breeders, and 377 (47%) had successful breeders.

During the last decade, the density of Willow Ptarmigan in my study area fluctuated from exceptionally low to exceptionally high, providing an opportunity to monitor the response of the Gyrfalcon to its highly variable food supply. A few years after the population collapse of the main prey species, it seems clear that these changes in prey density had a very strong influence on the breeding productivity of the Gyrfalcon population as a whole. It also seems clear that such a collapse of the ptarmigan population as seen in recent years in Lapland must also lead to increased mortality of adult falcons, and a decline in total population size in the near future (Koskimies and Ollila 2009).

In 2009–2010, during the exceptionally low density of Willow Ptarmigan, only about one third of the territories were occupied by a falcon or a pair at the beginning of the nesting season compared to up to twice as many in previous years. Half of the territories seemed to be without inhabitants during mid-winter, too. These observations suggest a marked decline of the total population. I do not know whether the missing falcons starved or moved more or less permanently to other areas. The total number of Gyrfalcons ringed as nestlings in Finland from the year 1913 to 2010 is only 350, and the number of ring recoveries is 11 (Valkama 2011). Almost all the ring recoveries were juveniles or 1–2 year-olds on the North Norwegian coast, west or northwest of the ringing sites. Only a few Gyrfalcons at most are yearly reported in Central or South Finland from autumn to winter by tens of thousands of bird watchers (Koskimies unpubl.). Even so, juvenile Gyrfalcons likely move to the Norwegian coast for winter, and adults may do so as well during winters when Willow Ptarmigan density is at its lowest. During such lows, there are very few incidental observations of wintering Gyrfalcons in my study area made by local bird watchers, hunters, reindeer herders or other field-oriented persons who report their records fairly actively. When the territory-owners have difficulty surviving within their familiar territories, it is probable that their competitors find it equally difficult, so leaving the area when prey is scarce does not necessarily risk the loss of a breeding territory. The same may hold true for the Golden Eagle in northern Lapland, another top predator dependent on Willow Ptarmigan as an important prey during wintertime. Eagles have been observed much less frequently in poor ptarmigan winters even on the carcasses of reindeer and other large mammals provided by nature photographers (Koskimies unpubl.).

Long-term Population Changes of the Gyrfalcon in Northern Fennoscandia.—It is generally believed that the Gyrfalcon population in Finland and other parts of northern Fennoscandia has experienced a marked declined since the 1800s due to intensive egg-collecting, persecution, and possible decrease of ptarmigan densities (e.g., Rassi et al. 1985, Tømmeraas 1993, 1994, Lindberg et al. 2010). These conclusions have been based, however, on more or less anecdotal evidence, generalized and qualitative descriptions of the occurrence of the Gyrfalcon in fairly small and non-representative areas. Most of the old descriptions are subjective, and even if they deal with a large area, the annual numbers of nests found by researchers like Sjölander (1946) and Wolley

(Newton 1864–1907) were based on unsystematic field-work compared with modern methods that include information also on unoccupied territories. Nor do the old sources give convincing information on the degree of effort expended in looking for nests.

Despite the methodological difficulties in comparison with old and present data, Tømmeraas (1993, 1994) tried to evaluate population change of the Gyrfalcon in northern Fennoscandia in a quantitative way. In one year in the early 1990s, he surveyed 29 nest sites which had been occupied by Gyrfalcons in western Lapland and Finnmark in the mid-1800s according to egg-collectors (Newton 1864–1907). Tømmeraas found falcon pairs nesting in only three of those same cliffs in a single year, and signs of Gyrfalcon presence in previous years at three other sites, and concluded that the population had declined by more than 80% during the 140-year period. He repeated the assertion of population collapse in subsequent publications (Tømmeraas 1998, 2004) and was cited by Holmberg and Falkdalen (1996).

The conclusion of population decrease by Tømmeraas (1993, 1994) stemmed from invalid methodology and non-representative sampling. First, as my study in the same region shows, Gyrfalcon pairs do not breed every year, especially if the densities of Willow and/or Rock Ptarmigan are at a low level. Every year a significant proportion of territorial birds remain non-breeding, even for many consecutive years. If a researcher were to survey nest sites in my study area in a single year, the number of pairs or occupied territories would not necessarily represent the actual population. During the last 20 years, I have found several territories with only one or two years with breeding and with birds leaving only vague evidence of falcon presence in various parts of the territory. Some territories, occupied in the early 1990s, remained without a single sign of a visit by a Gyrfalcon for up to a decade, and then abruptly a pair appeared and nested either once or during many consecutive years. In fact, many of the territories that Tømmeraas (1993, 1994) found vacant 20 years ago have had breeding pairs in later years.

Second, many pairs breeding in consecutive years often change nest sites, which makes it difficult to count the true number of breeding pairs if the entire study area is not thoroughly surveyed and every possible nest site checked. A high percentage of pairs have up to 3–5 alternative nests, and in some cases they occur as far as 10–17 km apart (Cade et al. 1998). Those nest sites used in the mid-1800s may have become unsuitable for several reasons in the course of 140 years (see also Johansen and Østlyngen 2011). Only a thorough search for all available nest sites within a territory could verify whether falcons really occupy the area or not. Thus, a straightforward comparison between single traditional nest sites then and now do not give a reliable estimate of a permanent change in the size of a population.

Third, neither Tømmeraas (1993, 1994) nor the egg-collectors in the mid-1800s systematically surveyed a defined area where they should have examined all territories every year from the beginning of the nesting season. The nest sites from old sources used by Tømmeraas (1993, 1994) were distributed in two different regions, the first along the River Kautokeinoelva in western Finnmark, and the second along the River Könkämaeno in the border area between Finland and Sweden. Nowadays, the first area is very thoroughly monitored by Johansen and Østlyngen (2011), and the second by myself. Tømmeraas (1993, 1994) counted the nest sites in these two separate areas together and treated them as a single area, although there was no proof that, in either the first or the second period, all of the territories were surveyed and all alternative nest sites checked, and that no other pairs bred close behind the borders, possibly having moved only a short distance from the classical site. The first area in Finnmark was more thoroughly studied and better covered by the egg-collectors and by Tømmeraas (1993, 1994), as clarified by Johansen and Østlyngen (2011), but the second area (nowadays within my study area) held many territories unknown both to egg-collectors in the mid-1800s and to Tømmeraas (1993, 1994) in the early 1990s (Koskimies unpubl.). Since the 1990s, many other previously unknown nest sites were occupied by Gyrfalcons within these two areas.

To conclude, the occupation of almost all classical territories known from the mid- and late 1800s, as well as many more previously unknown ones, makes me think that there could not at all be as marked a difference between the mid-1800s and the 1990s as suggested by Tømmeraas (1993, 1994).

Another unreasonable interpretation of long-term population decline is based on a comparison of the present densities of the Gyrfalcon with those seemingly high densities published by Sjölander (1946) from northern Sweden from surveys he conducted in the early 1900s (e.g., Cade et al. 1998, Potapov and Sale 2005). The true density of the Gyrfalcon nests found by Sjölander (1946), however, is not known, because he did not define exactly the size of his observation area, and it is interpreted by later researchers more or less anecdotally and without any certainty (Johansen and Østlyngen 2011). The Gyrfalcon density reported by Sjölander (1946) especially in the first and second decade of the 20th Century may in fact have been higher than in an average year nowadays, but there existed a very high population peak of the Norwegian Lemming (*Lemmus lemmus*) during those years (especially in 1903, 1904, 1910). During such vole years, populations of ptarmigan and other ground-nesting birds are much above average, because predators concentrate on superabundant small mammal populations (e.g., Steen 1989, Pedersen and Karlsen 2007). Gyrfalcon populations were probably denser during those years, when, for example, Suomalainen (1912) saw, in summer 1909, 26 eggs obtained during the previous spring by one egg-dealer based in Karesuando, a village at the Swedish–Finnish border, at the southern border of my present study area, and the southern border of the area studied by Sjölander (1946) (see also Cade et al. 1998). Also the size of the area from where the eggs seen by Suomalainen (1912) were obtained is not known (the same problem as with Sjölander 1946). Suomalainen (1912) reported that 800 eggs of the Snowy Owl (*Bubo scandiaca*) from over 100 nests were also collected along the River Könkämaeno in 1907 (partly the same area where Sjölander looked for Gyrfalcons) by a single man and his family around the village Vittanki, 30 km southeast of Lake Kilpisjärvi. This suggests an exceptionally high Lemming density during those years, as also suggested by the report of many other nests of the Snowy Owl by Suomalainen (1912) up until 1909.

A reliable density estimate of a Gyrfalcon population requires at least a decade-long and spatially extensive study with all possible territories and nest sites surveyed systematically In parts of the study area of Tømmeraas (1993, 1994), for example, the present population is markedly larger and more dense than he described 20 years ago after single-year surveys of a fraction of territories. In addition to pairs likely missed by him, many new ones have actually settled in territories which were unoccupied for years or even decades. Neighboring pairs have subsequently nested in several instances only within 6–10 km from each other as noted in the mid-1800s. Also, in many parts of the Gyrfalcon's range in the absence of human influence, the recorded density has never been higher (Clum and Cade 1994, Cade et al. 1998, Potapov and Sale 2005, Booms et al. 2008). Tømmeraas (1994) most probably also exaggerated the long-term decline of Willow Ptarmigan populations. In northern Finland, for example, in the mid-2000s, the density of ptarmigan reached peaks never seen since the mid-1900s (Helle and Wikman 2006).

Threats and Conservation Measures of the Gyrfalcon Population, and Priorities for

Future Research.—Despite the controversial views on long-term population change of the Gyrfalcon in northern Fennoscandia (Tømmeraas 1993, 1994, 1998, Cade et al. 1998, Koskimies 2006a), the species is likely vulnerable because of its restricted range, low breeding density, and high rate of specialization on prey and nest sites (Koskimies 1999, 2006b, Booms et al. 2008, Koskimies and Ollila 2009).

Inland in northern Fennoscandia, Gyrfalcons are almost totally dependent on one or two ptarmigan species for over-wintering, and the same one or two species form about 90% of prey items throughout the breeding period (Koskimies and Sulkava 2011). The current Willow and Rock Ptarmigan populations seem to be, on the average, at a lower level than before the mid-1930s, and the periods with low densities are repeated more often and last longer (Pedersen and Karlsen 2007). A significant reason is probably the expansion and population increase of the Red Fox (*Vulpes vulpes*) and other mammalian general predators, both in lowland birch forests (main habitat of the Willow Ptarmigan) as well as on the alpine tundra of the Scandinavian mountains and fell tops in Lapland (habitat of the Rock Ptarmigan). Climatic and environmental changes, leading to higher, denser, less optimal birch woods for Willow Ptarmigan, as well as excessive hunting may have a further negative effect on ptarmigan populations (Steen 1989, Holmberg and Falkdalen 1996, Hörnell-Willebrand 2005, Brøseth et al. 2005, Pedersen and Karlsen 2007, Brøseth and Pedersen 2010, cf. Barth 1881).

Rock Ptarmigan probably fluctuate less than Willow Ptarmigan (e.g., Väisänen et al. 1998, Pedersen and Karlsen 2007), but since the late 1990s, Rock Ptarmigan seem to have declined in numbers dramatically and permanently, at least locally, in Sweden and Norway (e.g., Tjernberg 2010). The Rock Ptarmigan is the main food for Gyrfalcons high in the Scandinavian mountains (Nyström 2005, Nyström et al. 2005). Along the coast of Norway and Kola Peninsula, falcons hunt waterfowl, waders, and other seabirds, too (e.g., Cade et al. 1998), many of which have increased in numbers. Thus, concerning food availability, coastal falcons are in a better position year round compared to their conspecifics living inland. Ekenstedt (2008) noted a larger decline both in the number of pairs and breeding success of the Gyrfalcon in Kirunafjällen, the sub-area in Norrbotten where ptarmigan hunting is allowed, compared to the other sub-area situated in the National Parks where hunting is prohibited. Whether lack of food explains this difference has not yet been proven, but it may be at least one cause for the difference.

Optimal nest sites, i.e., abrupt cliff faces with Raven nests, are also in short supply in many regions within the North Fennoscandian lowlands. Gyrfalcons also belong to the group of the arctic bird species that are expected to lose a great part of their present range, if climate change continues according to recent prognoses (Huntley et al. 2007). Because of these and many other threats, the Gyrfalcon has been classified as endangered in Finland (Rassi et al. 2010) and vulnerable in Sweden (Lindberg et al. 2010). In the Kola Peninsula, it is rare and in need of special protective measures (Koskimies and Kohanov 1998, Ganusevich 2001). In Norway, the Gyrfalcon is classified as NT (Near-Threatened, a species close to the qualifying criteria for Vulnerable) because of fairly large total population according to the newest revision of the population estimate (Kålås et al. 2011). The European Union regards the Gyrfalcon as a priority species in need of special conservation concern (listed in Annex I of the EU Birds Directive from 1979, BirdLife International 2004). The exceptionally large-scale and strong population collapse of Willow Ptarmigan reminds us also of the difficulties in evaluating the threat and conservation status of the Gyrfalcon without taking into account a longer-than-usual time perspective (Koskimies and Ollila 2009).

According to the EU Action Plan, compiled by the world experts on the Gyrfalcon, for example Tom Cade, Ólafur Nielsen, Eugene Potapov and others, the most important threats to the Gyrfalcon in northern Europe are lack of undisturbed nest sites and the possible decline of Willow and Rock Ptarmigan densities to the critical level (Koskimies 1999), as well as climate change (Huntley et al. 2007), the probable effect of which could not be evaluated in the late 1990s for the Action Plan. These threats were nevertheless classified as of high priority (Table 2, modified by Koskimies 2006b), and there are no reasons to change the evaluation according to data from field studies since then.

The conservation measures with highest priority include the following (Koskimies 1999, 2006b, Table 2):

- compiling both national and regional conservation management plans to guide practical work
- including territories in protected areas to offer legal status to them
- increasing food supply by protecting productive habitats for ptarmigan, by hunting regulation, and by other measures
- improving the availability and quality of nests by protecting Raven populations e.g. with carcasses as winter food, by building artificial nests, and by site-specific management in order to prevent non-intentional disturbance by hikers and other people
- continuing present monitoring projects of Gyrfalcon populations and initiating new programs in poorly known areas
- intensifying monitoring of population parameters, especially survival, dispersal and turnover rates, for purposes of reliable analyses of population viability and factors limiting the size and renewal of populations.

Lastly, to highlight the international scale of Gyrfalcon conservation, a species threatened by climate change, I must stress again the importance of proper studies on the ecology of the species and on scientifically valid monitoring methods throughout its range by referring to the similar views of Booms et al. (2008). They stress the following points as the main problems with respect to effective conservation, first of all because of lack of knowledge on vital population parameters:

- The Gyrfalcon's "...relative inaccessibility has left many aspects of its biology unstudied."
- "…sample sizes of Gyrfalcon studies have been very small, often fewer than 10 nests or individuals."
- "Information on survival rates, longevity, the timing and direction of dispersal, nest site fidelity, and the degree and nature of adult migration is severely lacking."
- "Almost no information exists on the presence, size, or ecology of the non-breeding population."

According to Booms et al. (2008), a serious problem for conservationists is the lack of knowledge on population regulation and size:

- "Another area of continuing controversy is the nature and cause of annual fluctuations in breeding populations of Gyrfalcons and what factors cause populations to fluctuate (or not) differently. This continues to be a problematic area for research because of the long-term, large scale commitment of resources necessary to address the issue properly."
- "Another more basic problem is achieving accurate population estimates. Although a number of researchers expend considerable effort to monitor populations, all agree that a large portion of potential Gyrfalcon habitat remains unsurveyed."
- "Current survey techniques rarely incorporate measures of detectability, forcing monitoring programs to rely on indices of population change instead of actual estimates."

Past research on the population ecology and monitoring of Gyrfalcons in northern Fennoscandia has yielded important data for conservation purposes, part of which can be adapted to other parts of the species' range. In our study areas here, we have exceptionally extensive data, both past and present, as well as extensive study areas providing various conditions for the falcons (e.g., from coastal cliffs with diverse prey sources to inland areas with one or two main prey species). This work forms a firm ground for future efforts which should be directed especially to those problematic topics listed by the EU Action Plan (Koskimies 1999, 2006b), as well as by Booms et al. (2008) from a North American perspective.

In northern Europe, the Species Action Plan sets the guidelines for the prioritization of the conservation and biological studies. Northern Fennoscandia, from North Norway and Sweden to North Finland and the Kola Peninsula, probably holds 5-10 percent of the world population estimated roughly at about 10,000 pairs (Potapov and Sale 2005). This area is also unique within the Gyrfalcon's range as, because of the mild climate due to the Gulf Stream, human density is higher than in comparable latitudes in Russia, Greenland, and North America. With more versatile economic activity, there is a greater variety of threats to the Gyrfalcon population in northern Fennoscandia than in other parts of the Gyrfalcon range.

In addition to evaluating the human-caused changes in the arctic and subarctic environment, it is necessary for scientists and managers, responsible for the conservation of Gyrfalcon populations, to analyze all the critical factors determining their viability, e.g., choice of habitat and prey, availability of prey species throughout the year, availability, abundance, and quality of nest sites, reproductive success, and survival (Koskimies 2006a, 2006b, Table 2).

Acknowledgments

Many people have helped me during the last 20 years when building up my knowledge on the Gyrfalcon and my extreme love for both this magnificent creature and its wild, untamed world. First and most heartily, I want to thank my dear friend Björn Ehrnsten, who has accompanied me during 17 years in the field on skis from the coldest and darkest mid-winter nights to the hottest summer days along daily marches of 30–55 km, day after day, for weeks. Matti Mela and Tuomo Ollila from Metsähallitus have been top-class colleagues in our joint effort to monitor the total Finnish population during the last decade, and Jari Kangasniemi, Petteri Polojärvi and Risto Korkalo have been their tough field assistants. Prof. Emeritus Seppo Sulkava, with his vast experience, identified ca. 6,000 prey items. My colleagues abroad, especially Tom Cade, Johan Ekenstedt, Ulla Falkdalen, Kenneth Johansen, Trond Johnsen, Ólafur Nielsen, Karl-Birger Strann and Arve Østlyngen have engaged in all kinds of common endeavors with the Gyrfalcon, both in the field and indoors, and were always willing to share their time and friendship, views and experiences as much as I could ever hope. My sincere thanks go also to Rick Watson and Grainger Hunt for reviewing and editing my article and giving good advice for clarifying the text. Last, but not least, I want to thank my wife Irma and my children Inari, Iiris, Aarni and Otso for letting me devote my time and activity to the falcons and wild nature in the far Lapland for up to two months per year.

Table 2. Threats, conservation measures and research needs of the Gyrfalcon in northern Fennoscandia (importance in parenthesis according to Koskimies 1999, 2006b: I = high, II = medium, III = low). This list includes only the most important threats in Fennoscandia and special research needs for addressing them more properly. In addition, population dynamics of the Gyrfalcon (population size, natality, mortality, movements) should be an integral part of research and monitoring.

Threats	Conservation measures	Research needs
Reduced prey numbers (I)	**Grouse conservation**	**Food availability**
hunting	hunting regulations	Grouse abundance
degradation of habitat	protected areas	effects of hunting
disturbance	land use planning	food of falcons
mammalian predators	trapping of other predators	
reindeer fences		
Disturbance of nest sites (I)	**Land use planning**	**Susceptibility to disturbance**
snow mobile traffic	snow mobile routes	quality of nest sites
ecotourism	tracks, skiing routes	use of artificial nests
hiking	cottages, huts	
bird watching and photographing	photography licenses	
rock climbing	education	
	artificial nests	
Habitat destruction (II)	**Habitat protection**	**Habitat quality**
new roads	protected areas	use of habitat
snow mobile routes	management of other areas	critical habitat needs
tourism infrastructure		
cottages		
reindeer fences		
powerlines		
Robbing of nests (II)	**Concealing of nests**	**Falcon trade**
egg-collecting	wardening	captive breeding
falconry	education	DNA-identification
falcon production in captivity (incl. hybrids)	artificial nests	
Shooting adults, destroying nests (III)	**Education**	**Attitudes by public**
game keeping	wardening	
Reduced Raven nest numbers (III)	**Artificial nests**	**Artificial nests**
decline of Raven population	feeding of Ravens	Raven monitoring
		availability of nat. nests
Collisions (III)	**Land use planning**	**Susceptibility**
reindeer fences		
powerlines		
Chemical contamination (III)	**Reducing of chemicals**	**Analysis of chemicals**
long-distance fallout		
waterfowl (esp. coastal in winter)		

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